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CIRCULAR No. 442 September 1937
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MOSAIC DISEASES OF WHEAT AND RELATED CEREALS

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INTRODUCTION

Mosaics have been appearing on wheat in new localities for several years, and growers, as well as agricultural specialists, have come to realize that these diseases constitute a menace to wheat production in certain areas.

As earlier publications on the subject are out of print, it seems advisable to present certain information that has appeared previously, as well as some that is new. Although the studies on the several wheat viruses are not complete, this circular makes the latest information available to growers and crop specialists, as well as to research workers.

Since much of the actual testing for resistance and susceptibility to the diseases has been cooperative, the results of these tests and the major discussion of control are not included in the present publication.

HISTORY

Wheat mosaic was first observed in the United States early in the spring of 1919 in fields of winter wheat in the Mississippi River bottoms near East St. Louis and Granite City, Ill. Later that year the disease was found in several counties in other parts of Illinois and in Indiana. At that time the disease was designated as take-all. However, experimental tests (*2*)[2] and observations soon indicated that it was not the take-all disease, and accordingly it was designated by

[1] The writer wishes to acknowledge the assistance of Matthew Koerner, who recorded much of the experimental data and who, with Walter Marcey, assisted in the field tests at the Arlington Experiment Farm, Arlington, Va., and carried out much of the inoculation work. Acknowledgment is also due to Benjamin Koehler, S. G. Lehman, Ralph M. Caldwell, Hurley Fellows, C. O. Johnston, L. E. Melchers, and G. L. Peltier, in connection with the making of field surveys and supplying information and materials, and to L. W. Boyle for assisting in the operation of the controlled-temperature chambers.

[2] Italic numbers in parentheses refer to Literature Cited, p. 22.

the name "rosette disease." As the investigations progressed it became apparent that rosette is a phase of a mosaic (*3*, *5*, *6*) and that several mosaics occur on wheat in the United States.

Mosaic was first reported as such on wheat in the Great Plains area in 1922 by G. L. Peltier [3] in experimental plots at Lincoln, Nebr. Since that time Peltier has shown the writer scattered wheat plants with yellow mosaic and many wheat plants with green mosaic at and near Lincoln.

In the spring of 1929 Hurley Fellows and C. O. Johnston called the writer's attention to a yellow mosaic on scattered wheat plants in experimental plots at Manhattan, Kans. In 1930 Melchers and Fellows [4] reported mosaic in many wheatfields in northwestern Kansas, and in 1932 [5] it was reported in fields in Dickinson and Saline Counties, Kans.

DISTRIBUTION

The distribution of wheat mosaics by counties and States is set forth below and is also shown in figure 1. The greatest number of

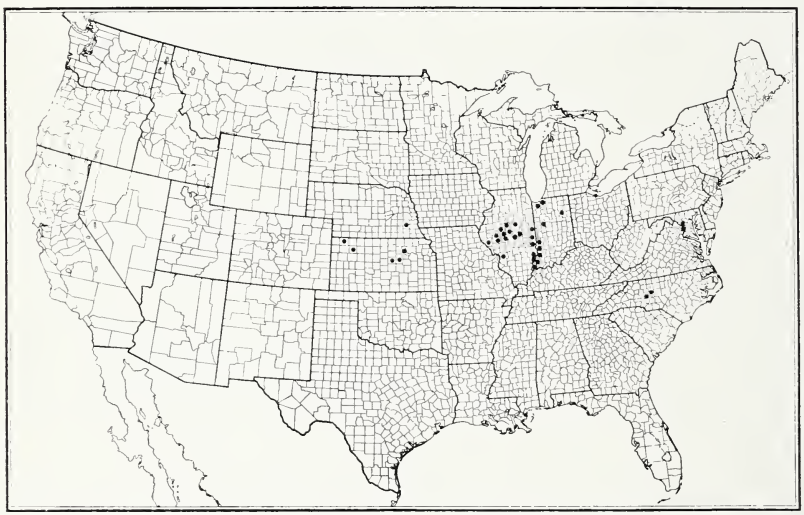

FIGURE 1.—Map of the United States, showing the geographic distribution of wheat mosaic by counties.

infested areas occur in Illinois and Indiana, in the order named. Each season new locations have been reported. In 1936 wheat mosaic was found in five counties in Illinois and four counties in Indiana from which the diseases had not been reported previously.

[3] HASKELL, R. J., and WOOD, J. I. DISEASES OF CEREAL AND FORAGE CROPS IN THE UNITED STATES IN 1922. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bull. Sup. 27: 164–226, illus. 1923. [Mimeographed.]

[4] MELCHERS, L. E., and FELLOWS, H. WHEAT MOSAIC IN KANSAS. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr. 14: 158. 1930. [Mimeographed.]

[5] MCKINNEY, H. H. WHEAT MOSAIC IN KANSAS. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rptr. 16: 115–116. 1932. [Mimeographed.]

Distribution of wheat mosaics in the United States

State and county	State and county	State and county
Illinois:	Illinois—Con.	Kansas:
Cass.	Tazewell.	Dickinson.
Clark.	Vermilion.	Rawlins.
Edgar.	Wabash.	Riley.
Lawrence.	Indiana:	Saline.
Logan.	Gibson.	Sheridan.
McLean.	Huntington.	Maryland:
Macon.	Knox.	Montgomery.
Madison.	La Porte.	Nebraska:
Mason.	Porter.	Lancaster.
Menard.	Posey.	North Carolina:
Piatt.	Sullivan.	Davidson.
Pike.	Tippecanoe.	Rowan.
Sangamon.	Vigo.	Virginia:
Scott.		Arlington.

After this paper went to press wheat mosaic was reported from Brown, Fulton, Peoria, Schuyler, Scott, and Woodford Counties in Illinois, and from Fountain and Vermillion Counties in Indiana.

ECONOMIC IMPORTANCE

From the standpoint of the national wheat crop the importance of the mosaics is potential, but in the areas east of the Mississippi River where the diseases occur it is not uncommon to see entire fields of winter wheat rendered worthless. In other instances the destruction is partial, slight, or imperceptible.

Losses of economic importance have not been reported from counties in Nebraska nor from Riley County, Kans. Severe losses amounting to total crop failure were observed by L. E. Melchers and Hurley Fellows in Rawlins and Sheridan Counties, Kans., in 1930, and the writer observed a complete loss of the crop in one field in Saline County, Kans., in 1932. Plants in small areas in several fields were badly infected in Dickinson County, Kans., in 1932.

RECURRENCE AND SPREAD

Mosaic-rosette and at least certain of the yellow mosaics which occur east of the Mississippi River are spread by means of infested soil (*2*), and another wheat mosaic is spread by means of the rhizomes of *Agropyron repens* (L.) Beauv. Many tests have been carried out to determine whether aphids or other flying insects transmit the viruses of these eastern mosaics, but thus far the results have been negative. Soils from infested areas have been transported into areas where wheat mosaic is not known to occur naturally, and mosaic has appeared the following spring in wheat planted in such soils. The disease also has occurred in plants grown in these infested soils in insect-free culture chambers.

These mosaics have recurred more regularly and over longer periods in heavy soils than in the sandy soils. The exact relationship between the viruses and the soil is not known. It is possible that some insect or other organism may carry the virus in the soil and serve as an infecting agent or vector.

There is no evidence that the recurrence of the disease is correlated with cropping methods. Heavily infested gumbo soil from Granite City, Ill., kept in a dry condition in the laboratory for 3 years was

still infectious and induced mosaic-rosette in a high percentage of the wheat plants grown in it.

Several fields near Granite City, Ill., were under observation from 1919 to 1926, and each year when susceptible wheat was on the land mosaic occurred. In 1927 some of these fields showed a noticeable decline in the amount of mosaic. In the spring of 1936 many of these fields were examined, but owing to the fact that growers are using resistant or tolerant varieties it was difficult to find the disease. However, mosaic was found in some fields.

Mosaic recurs from year to year in a small way near Manhattan, Riley County, Kans., and near Lincoln, Lancaster County, Nebr., and possibly in other areas, but it is noteworthy that these western mosaics do not recur with certainty. Fields showing total crop destruction in Rawlins, Sheridan, and Saline Counties, Kans., were free from mosaics the seasons following the destruction of the crop.

There is no positive evidence that the viruses of the western mosaics are carried in the soil. Soils in which mosaic-diseased plants were growing have been collected from several areas in Kansas, and the seed from susceptible wheat has been planted in them the following season out of doors and also during the same season in culture chambers at the Arlington Experiment Farm, Arlington, Va. In all cases these soils failed to induce mosaic. This is distinctly at variance with the situation prevailing with the wheat mosaics occurring east of the Mississippi River.

Peltier [6] reported the transfer of a wheat mosaic occurring in Nebraska by means of an unidentified species of aphid, and later the writer transmitted a wheat mosaic collected at Salina, Kans., by means of an unidentified aphid. A few aphids were present on diseased plants which were shipped from Kansas to Arlington Farm in the late spring. These were transferred to healthy plants and one plant developed mosaic. The aphids were inadvertently lost during a routine fumigation. While these results are far from conclusive, there is reason to believe that some of the wheat mosaics in Kansas as well as in Nebraska are transmitted by certain aphids. Some species not especially common may serve as vectors. It is possible also that volunteer wheat or some other plant serves as a repository for the virus during the summer. In such case an adverse season might greatly reduce the amount of virus available for a vector, and subsequent wheat crops would fail to exhibit mosaic on a large scale.

CULTIVATED CROPS AFFECTED

In previous publications (*3*, *4*) it was pointed out that certain varieties of common, club, poulard, durum, and Polish wheats, and emmer, spelt, einkorn, rye, and barley are susceptible to the mosaics occurring in the eastern region. The diseases are of no consequence in spring-sown varieties, but certain spring varieties develop mosaics when sown in the autumn in a region of mild winters.

Peltier [6] transmitted one of the wheat mosaics occurring in Nebraska to corn by means of aphids and also extracted juice, and he transmitted it to healthy wheat by means of the extracted juice.

[6] HASKELL, R. J., and WOOD, J. I. See footnote 3.

CONTROL

In the case of the eastern mosaics the virus infestation can be eliminated from soils by treating with commercial formalin diluted in 49 parts of water, as described in an earlier publication (*2*). However, this method is too expensive for commercial application. Very early and very late sowing (*2*, *17*) reduces or controls these mosaics, but this method cannot be recommended because of hazards from other factors, such as hessian fly and winter injury. The mosaics occurring east of the Mississippi River are controlled commercially through the use of resistant or tolerant varieties and selections (*2*, *18*). Figure 2 illustrates a strain of Harvest Queen wheat selected for its resistance to mosaic-rosette.

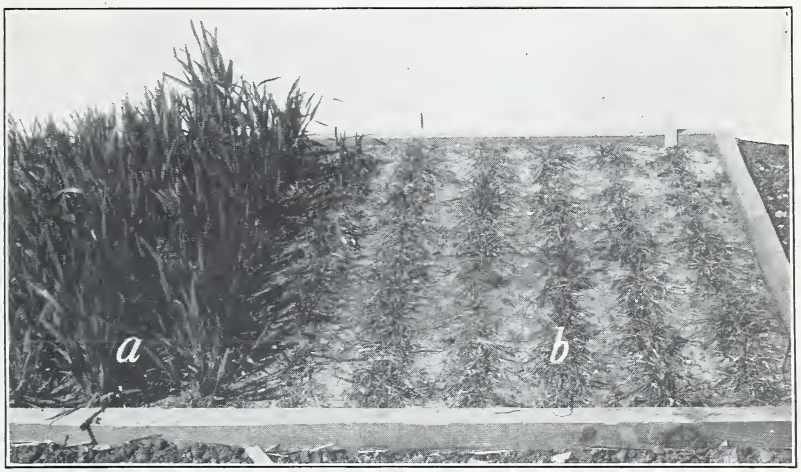

FIGURE 2.—Harvest Queen wheat selections: The five rows at *b* were a strain selected for high susceptibility to mosaic-rosette; the two rows at *a* were a strain selected for resistance to mosaic-rosette. The seeds were sown in the autumn in virus-infested field soil which was uniformly mixed before sowing. (Photographed Apr. 18, 1928.)

Since the western wheat mosaics have not recurred with regularity, it has not been possible to determine the mode of their spread nor the means of control. Extensive series of wheat varieties and hybrids were sown by Fellows near Atwood and at Salina, Kans. These sowings were made in areas where the crop was completely destroyed by mosaic the previous season, yet no signs of mosaic appeared in the test material or in commercial wheat the following season. No outstanding instances of wheat mosaic have been reported in Kansas since 1932.

DESCRIPTION OF THE DISEASES

The symptoms induced by a given virus are influenced by soil fertility, temperature, light, age of the plant, and by the variety and species of plant that is infected. In general, mosaic mottling tends to be reduced when chlorophyll production is favored in the diseased plant by soil fertility or other factors in the environment.

In critical studies on the differentiation of viruses and especially some of the mutants, the environment, particularly temperature and light, should be controlled as far as practicable. By manipulating

environmental factors over suitable ranges it is often possible to differentiate viruses on a given plant genotype (*7*) and to greatly enhance the value of cross-inoculation studies on different varieties and species.

In describing the following mosaics it is not the aim to describe any one type on a wide range of plant varieties or in a great number of environments, but rather to indicate simply the chief difference between the mosaics when maintained in plant-culture chambers,[7] in greenhouses, and when possible to describe them under field conditions. Unless stated otherwise, the comparisons were made at temperatures near 60° F. in an 8-hour daily photoperiod on Harvest Queen winter wheat 3 to 4 weeks after the first signs of symptoms, and the common names used for the mosaics are based on these conditions, which are termed "standard conditions." This temperature and photoperiod were used because they favor infection, and they are near optimum for the normal development of the plant during the leaf-and-tiller-formation phase (*10*, *11*, *17*).

All the Harvest Queen wheat seed used was from a special selection which is highly susceptible to mosaic-rosette (fig. 2).

Seeds were sown in 6-inch pots at a rate necessary to insure 15 to 20 seedlings. These pots were kept near 60° F. with an 8-hour day. When the seedlings had developed from two to three leaves they were removed from the soil, and all soil was carefully washed from the roots. The seedlings were then inoculated and replanted in soil, four seedlings in a 6-inch pot.

Inoculum was obtained from leaves showing the typical signs of disease. The leaves were clipped into short pieces and pulped with quartz sand in a laboratory mortar; sufficient sterile distilled water was added to produce a watery mass. This inoculum was introduced into the plants by the following methods:

(1) Dropped into the unrolled central leaves, followed by pricking the leaves through the drop of inoculum. This method was very unsatisfactory and was discarded. The leaves are so small that the drop of inoculum will not flow into the unrolled leaves with certainty.

(2) A washed seedling is laid across a small watch glass containing the inoculum, and the crown region is pressed into the inoculum. The base of the leaf sheaths is submerged and gently pricked several times through the inoculum. A small piece of cotton lint is then wrapped around the punctured region, and the seedling is replanted.

(3) Carborundum powder (370-grain), as recommended by Rawlins and Tompkins (*14*), is put in the inoculum. The thumb and fingers of the operator are dipped into this mixture and the distal halves of two or three leaves are carefully rubbed, in order to introduce the virus without killing the rubbed portion immediately.

All of the diseases described in this circular are designated mosaics of one type or another; however, two of the viruses induce streaking and striping to a marked degree and under certain conditions may be classed as streak or stripe diseases; therefore, these diseases are referred to as streak-mosaics. They are not designated as streaks outright because some mosaic mottling is sometimes present and because different degrees of streaking, striping, and banding occur.

[7] Virus cultures were maintained in plant-culture chambers in which the mean temperatures were maintained as near 60° F. as possible and the daily photoperiod was held at 8 hours. Day temperatures went above 60° when the sun was bright, but rarely went to 70° at midday. During moderate light and at night the temperature was at or very close to 60° except during a break-down of the equipment. The chambers were located out of doors and received unobstructed daylight which passed through two panes of single-strength flat-drawn window glass with air space between (*10*).

GREEN MOSAIC OR MOSAIC-ROSETTE (WHEAT VIRUS 1)

Under field conditions mosaic mottling sometimes appears on a few plants in the late autumn, but it is not abundant until the new leaves develop in the spring. In spring-sown Harvest Queen wheat mosaic mottling occurs on a few plants if the season is cool for a long period, but rosette does not occur under these conditions.

Rosette appears in the spring when the healthy plants are beginning their spring activity. The rosetted plants remain short, new side shoots or tillers develop, sometimes in great abundance, and these do not elongate normally; as a result the plants take on a bunchy appearance, as illustrated in figures 2, 3, 4, 5, and 6. The plants show

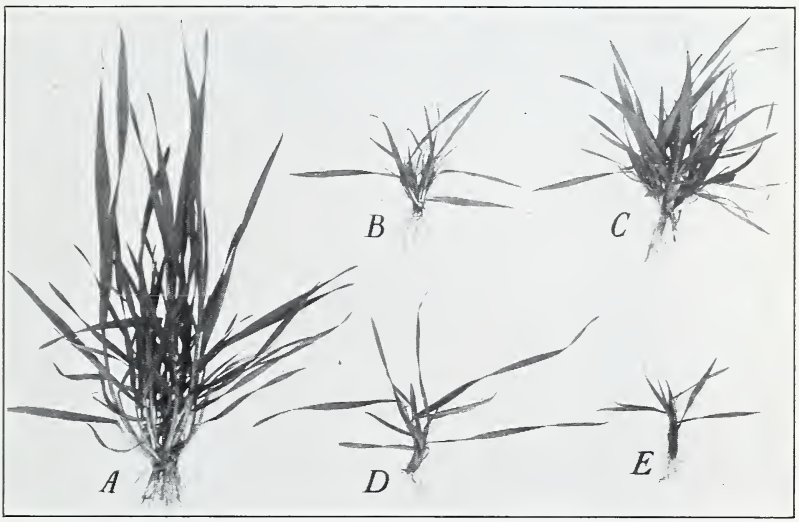

FIGURE 3.—Mosaic-rosette (virus 1) on Harvest Queen wheat grown under standard experimental conditions: *A*, Healthy plant; *B*, *C*, *D*, and *E*, plants showing several expressions of rosette grown simultaneously and in the same chamber with plant *A*. The healthy plant and the diseased plants are typical examples of plants in the field during the spring in noninfested and in infested soils, respectively. The virus represented a purified source of virus 1 and was introduced into healthy seedlings by means of needles, as described in the text.

mosaic mottling which later may become obscured under field conditions by an intense development of chlorophyll in the foliage. This causes the leaves to take on a bluish-green coloration resembling plants infested with the larvae and pupae of the hessian fly (*9, pl. 2; 12, pl. 1*).

Mosaic-rosette frequently occurs in limited areas or patches in infested fields, as illustrated previously (*2, pl. 2; 9, pl. 1; 12, fig. 1*). These patches may be very small or large. Infested patches also occur in fields sown to varieties that manifest only the mosaic mottling, but these are not conspicuous unless the mosaic is especially yellow.

Rosetted plants are especially susceptible to the attack of soil parasites (*2, 12*). In certain areas, especially in heavy bottom lands, *Helminthosporium sativum* Pam., King, and Bak. induces a rotting at the base of the tillers. This condition is less evident in sandy soils. During a dry spring few spring tillers are produced by rosetted plants, and the plants usually die early. If the season is normal, spring-formed tillers usually produce small imperfectly filled heads. These appear late, usually when the healthy plants are ripening. During

FIGURE 4.—Harvest Queen wheat plants illustrating the difference in gross symptoms induced by mosaic-rosette (virus 1) and yellow mosaic (virus 3): *A*, Healthy plant; *B*, stunted plant with yellow mosaic, which sometimes induces more severe injury than is illustrated; *C*, extremely stunted rosetted plant with mosaic-rosette (virus 1). All plants were grown simultaneously under standard conditions for 25 weeks followed by 70° to 80° F. with a 16-hour day for 2 weeks before photographing. Inoculations were made with purified sources of the viruses by means of needles. These viruses were together in the original material collected. All plants were typical of similar plants in the field during the early jointing period.

cool moist seasons rosetted plants have been known in a few instances to recover in a surprising manner, but such cases are unusual.

The typical field plant symptoms of mosaic and rosette have been reproduced in Harvest Queen winter wheat grown in plant-culture

FIGURE 5.—Population of Harvest Queen wheat plants from an entire experiment grown simultaneously under standard conditions for 15 weeks followed by 65° to 90° F. with a 16-hour day for 3 weeks before photographing: *A*, Plants recovering from mosaic-rosette (virus 1); *B*, plants with yellow mosaic (virus 3); *C*, healthy plants.

FIGURE 6.—Harvest Queen wheat plants illustrating the difference in the gross plant symptoms induced by the light-green mosaic (virus 4) and mosaic-rosette (virus 1) when grown under standard conditions for 18 weeks followed by 70° to 80° F. with a 16-hour day for 2 weeks before photographing. Inoculations were made by means of needles, and purified sources of virus were used: *A*, Healthy; *B*, virus 4; *C*, virus 1.

chambers at temperatures near 60° F. and with a daily light period of 8 hours, hereafter referred to as standard conditions. The typical rosette symptoms obtained under these conditions are illustrated in figures 3, 4, 5, and 6. The roots and the tillers were free of the fungus

rots occurring in the field. Under standard conditions the virus reduces the chlorophyll in the foliage very slightly, inducing very mild light-green mottling, short dashes or streaks, and sometimes long streaks or bands parallel to the leaf axis, as illustrated in figure 7. Occasionally, normal green dashes and streaks appear in the wider light-green bands or zones, as illustrated in figure 7, *D*, and in another publication (*3, fig. 1, E*). Usually no more than 10 percent of the functioning leaves on a plant show reduced chlorophyll areas at one time, and the leaves retain the symptoms for a short time due to an

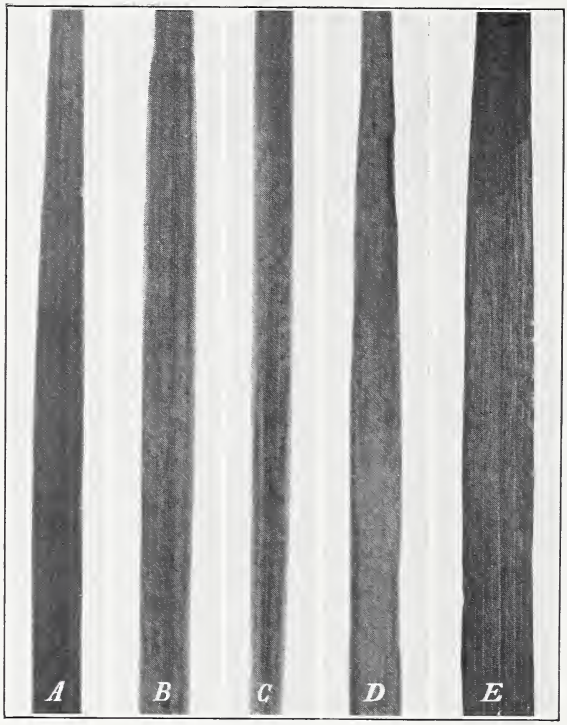

FIGURE 7.—Portions of leaves of Harvest Queen wheat, illustrating the foliage symptoms induced by mosaic-rosette (virus 1) under standard conditions. *A*, *B*, *C*, and *D* are from plants during the tiller-formation period; *A*, Healthy leaf; *B*, illustrates typical light-green mottling; *D*, illustrates the large proportion of mildly chlorotic tissue containing normal green dashes and short streaks; *C*, an intermediate condition in which light-green and dark-green streaks and short bands prevail; *E*, from a plant during the jointing period, showing mildly chlorotic mottling, short streaks, and dashes. During the jointing period the chlorotic symptoms resemble those induced by virus 2.

excessive appearance of chlorophyll. There is an excessive development of tillers and a stunting causing the rosetted appearance about 3 weeks after the first signs of mosaic.

Mosaic mottling appears at temperatures as high as 70° to 75° F. and as low as 40° to 50°, but the rosette symptoms do not develop throughout this entire range of temperatures. Long days—over 12 hours—likewise prevent the occurrence of rosette at temperatures near 60°. However, when virus of mosaic-rosette is recovered from the plants grown at temperatures favoring the expression of mosaic but not rosette, it induces typical rosette as well as mosaic in Harvest Queen plants when grown under standard conditions.

When this virus was first isolated in 1930, from 50 to 100 percent of the inoculated plants developed symptoms, but during the subculturing of the virus in Harvest Queen wheat it has become increasingly difficult to obtain infection, until at the present time the virus frequently fails to induce infection in a single plant in a series. Negative infection rarely or never occurs in an entire series when inoculations are made with the other viruses.

Many attempts have been made to isolate a virus from rosetted plants that will induce rosette without the mosaic, but this has been without success. On the basis of present evidence rosette is considered to be one expression of a mosaic on Harvest Queen and a few other varieties of winter wheat.

Most varieties do not express the rosette symptoms but do express the mosaic-mottling symptoms. In these cases the mottling may be a very mild green, a distinct green, a yellowish green, or a distinct yellow type, depending on the species, the variety, and the conditions of growth. Red Winter spelt expresses yellow mosaic when inoculated with wheat virus 1, but the degree of yellowing is slightly less than that induced by wheat virus 3. Spelt does not express the rosette symptoms.[8]

GREEN MOSAIC (WHEAT VIRUS 2)[9]

Green mosaic was first observed by Matthew Koerner on *Agropyron repens* in the mosaic experimental plots on the Arlington farm. It is not known to what extent this mosaic occurs on *A. repens* or on wheat in the field.

On *Agropyron repens* and on Harvest Queen wheat grown under standard conditions this virus induces a mild green mosaic. The degree of chlorophyll reduction and the mottling patterns resemble very closely those induced in Harvest Queen wheat by virus 1. Mottling persists in a leaf for but a short time, and it is usually most evident in the partially unrolled portions of leaves emerging from the sheaths (fig. 8). No rosette symptoms are associated with this mosaic on Harvest Queen wheat, thus differentiating the virus from that of mosaic-rosette.

Virus 2 persists in the underground stems (rhizomes) of *Agropyron repens*. Rhizomes from mosaic-diseased plants have been collected during the summer and stored in moist soil in darkness at temperatures slightly above freezing for 7 months. When placed under suitable conditions for growth the new foliage developed green mosaic.

This mosaic has been transmitted by artificial inoculations to healthy wheat and healthy *Agropyron repens*, but all attempts to transmit other wheat mosaics described in this circular to *A. repens* have met with failure, thus indicating further that wheat virus 2 differs from the other viruses under consideration.

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[8] During the spring of 1936 the writer observed for the first time mosaic on a few plants of *Bromus commutatus* Schrad. of the tribe Festuceae, which were growing in the virus-infested plots on Arlington farm. Of the 80 Harvest Queen wheat plants which have been inoculated with virus from this wild grass 32 developed mosaic-rosette, 8 developed yellow mosaic only, and 40 remained mosaic-free. This is the first case the writer has observed of a grass mosaic occurring naturally on a species outside of the tribe Hordeae in areas where winter varieties of wheat are grown commercially. However, the tribes Festuceae and Hordeae are considered to be very closely related botanically.

[9] A mosaic-infested patch of *Agropyron repens*, which has been under the writer's observation for several years, manifested the typical green mosaic until in 1936 a small area within the larger area was observed to exhibit a yellow-mosaic mottling. It is not known whether these symptoms are the result of another virus or of another strain of *A. repens*. It seems doubtful whether they were due to soil or atmospheric environment.

YELLOW MOSAIC (WHEAT VIRUS 3)

This yellow mosaic is associated with mosaic-rosette in the field. The virus was isolated in 1930 (*5*), and it has been maintained in wheat plants grown in culture chambers since that time. In the first isolations the virus of mosaic-rosette (wheat virus 1) was present, but in subsequent selection transfers virus 1 was eliminated. On Harvest Queen wheat grown under standard conditions from 95 to 100 percent of all the leaves show symptoms ranging from mosaic mottling, streaks, and stripes to almost a complete yellowing, as illustrated in figure 9 and in a previous publication (*3, fig. 1, F*). Usually from 25

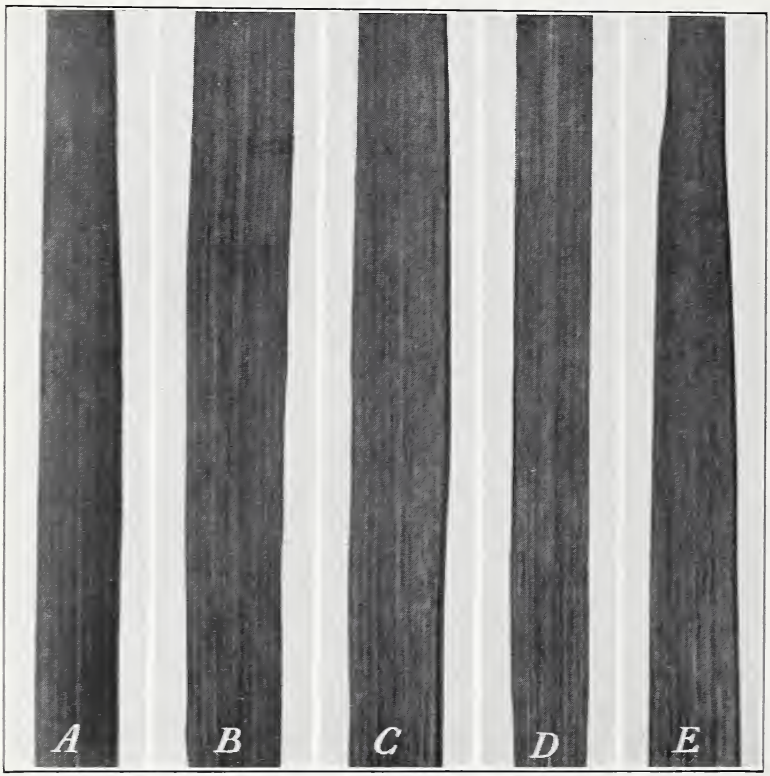

FIGURE 8.—Portions of leaves of Harvest Queen wheat, illustrating the foliage symptoms induced by green mosaic (virus 2) under standard conditions. *A*, Healthy leaf; *B*, *C*, *D*, and *E* illustrate mild mosaic mottling and faint streaking from plants in the jointing stage. During the tiller-formation period the mosaic symptoms are like those induced by virus 1, illustrated in figure 7.

to 40 percent of the diseased leaves show yellowing to some degree, whereas the remainder exhibit very light-green to yellow-green patterns. Plants become stunted (fig. 4, *B*) in varying degrees and sometimes are killed. The leaves sometimes remain in a rolled condition (fig. 9, *D*), resembling the leaves of wild garlic. The lower leaves turn yellow, wither, and die prematurely. Chlorophyll production usually is favored in the mottled tissues of new foliage as the surviving plants advance to maturity. This condition is favored by nitrogen-containing fertilizers. In comparison with virus 5, virus 3 induces severe yellow chlorosis in fewer leaves than the former. In comparison with

virus 7, virus 3 induces the mosaic mottling on more leaves and the long streaks, stripes, and bands on fewer leaves.

This virus does not induce rosette, but on Red Winter spelt grown under standard conditions it induces a severe yellow mosaic.

In the field yellow mosaics have been observed to produce symptoms very similar to those described above for temperatures near 60° F. In badly infested areas these plants give a wheatfield a yellow to yellowish-green appearance. When the areas are scattered over a field they give it a spotted appearance.

FIGURE 9.—Portions of leaves of Harvest Queen wheat, illustrating the foliage symptoms induced by yellow mosaic (virus 3) under standard conditions. Healthy leaves illustrated in figures 7 and 8 serve as controls for this figure. *A*, *B*, *C*, and *D* are from plants during the tiller-formation period; *E* and *F*, from plants during the jointing period. The lightest areas shown in these leaves were extremely yellow or they contained small traces of chlorophyll which was not evident except on close examination. *D* illustrates the extreme leaf rolling which sometimes occurs in this disease.

LIGHT-GREEN MOSAIC (WHEAT VIRUS 4)

The virus of light-green mosaic was obtained from mosaic-diseased wheat plants sent to the writer by L. E. Melchers. The plants were collected near Manhattan, Kans.

On Harvest Queen wheat grown under standard conditions the virus sometimes induces a mild-green mottling, but usually it reduces the amount of chlorophyll to a greater degree than viruses 1 and 2, thus causing a yellowish-green color of the affected areas.

On Harvest Queen wheat grown under standard conditions about 70 to 90 percent of the leaves on a plant show light-green to yellowish-

green chlorosis 3 to 4 weeks after the first signs of the disease. This chlorosis frequently involves all or a large portion of the leaf (fig. 10, *B*, *C*). A few normal green dashes or streaks occur in the light-green tissue, and light-green to yellowish-green dashes or streaks occur in the darker green marginal zones which blend into the lighter areas (fig. 10, *C*). A few leaves develop mosaic mottling in these marginal zones. In the jointing stage of the plant a few leaves show greenish-yellow to yellow dashes and streaks on a normal green background (fig. 10, *E*, *F*) and sometimes a typical light-green mosaic pattern.

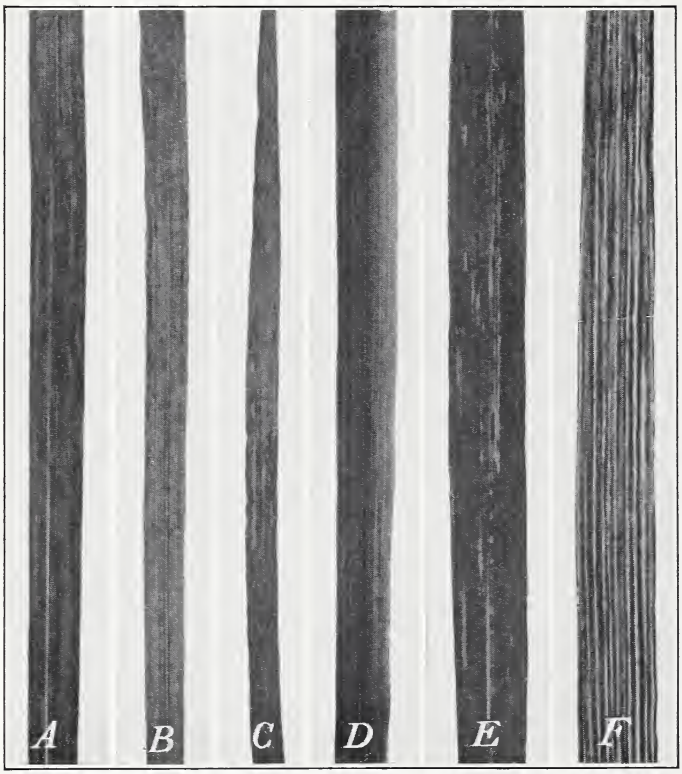

FIGURE 10.—Portions of leaves of Harvest Queen wheat, illustrating the foliage symptoms induced by light-green mosaic (virus 4) under standard conditions. Healthy leaves, illustrated in figures 7 and 8, serve as controls for this figure. *A*, *B*, *C*, and *D* are from plants during the tiller-formation period. *A* illustrates mottling, which is more distinct than that illustrated in figure 7, *B* and *C*, because of a greater reduction in chlorophyll; *B* and *C* illustrate large portions of light-green tissue containing a few normal green dashes; *D* illustrates a light-green band at one edge of the leaf; *E* and *F* illustrate yellowish-green and yellow stripes during the jointing period.

The majority of the leaves are normal green and show no mottling during the jointing stage. This virus stunts (fig. 6, *B*) but does not kill the plant, and it does not induce rosette. The marked tendency of leaves to express normal green dashes on a light-green background, as illustrated in figure 10, *B* and *C*, and the absence of rosette distinguish this green mosaic from green mosaic rosette (virus 1).

Virus 4 differs from virus 2 in that chlorosis is induced to a lesser extent in the latter, and virus 4 seems not to infect *Agropyron repens*. Long streaks, stripes, and bands, such as induced by viruses 6 and 7, are unusual in plants infected by virus 4.

At temperatures near 70° to 75° F. in a long day virus 4 induces a distinct yellow mottling and streaking in Harvest Queen.

YELLOW MOSAIC (WHEAT VIRUS 5)

The virus of yellow mosaic was isolated from mosaic-diseased wheat plants collected near Manhattan, Kans., by L. E. Melchers.

Under standard conditions the symptoms in Harvest Queen wheat are very similar to but more severe than those induced by virus 3. Virus 5 induces symptoms in 95 to 100 percent of the leaves, a greater number of these (50 to 60 percent of the diseased leaves) develop strongly yellow chlorotic areas and yellow mosaic mottling, streaking, and striping (fig. 11), leaf rolling occurs, plants are stunted and

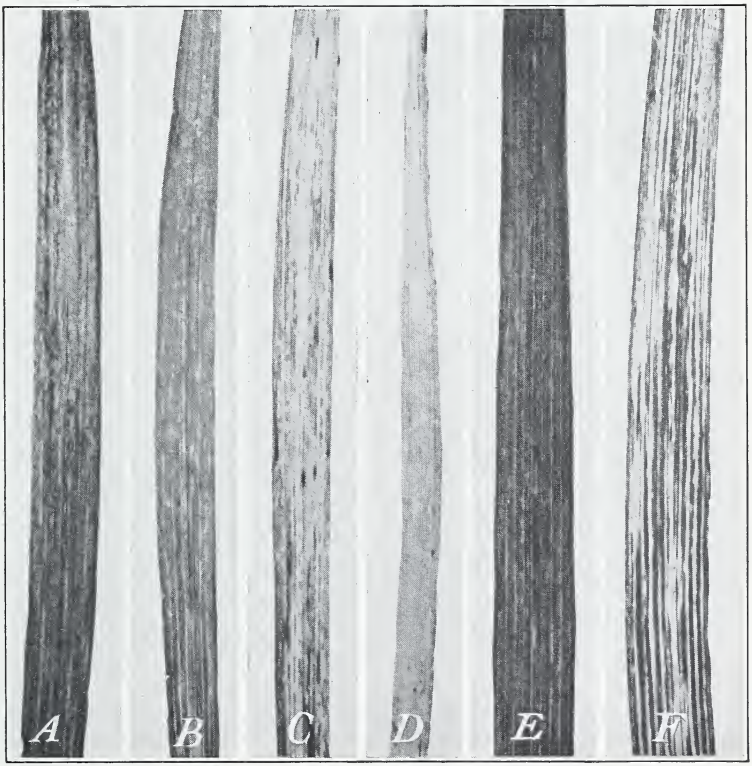

FIGURE 11.—Portions of leaves of Harvest Queen wheat, illustrating the foliage symptoms induced by yellow mosaic (virus 5) under standard conditions. Healthy leaves illustrated in figures 7 and 8 serve as controls for this figure. *A*, *B*, *C*, and *D* are from plants during the tiller-formation period; *E* and *F* are from plants during the jointing period. The lightest areas shown in these leaves were extremely yellow or almost white.

frequently killed while young, and under standard conditions many plants remain yellow during jointing, later dying without producing seed. This is the most severe of the yellow mosaics of wheat. The virus does not induce rosette.

MILD STREAK MOSAIC (WHEAT VIRUS 6)

The virus producing mild streak mosaic is one of at least two present in wheat plants collected from a field near Salina, Saline County, Kans.

The combined viruses wrought complete destruction of the crop of mixed Turkey, Kanred, and Jones Fife wheat in a 40-acre field and in a portion of an adjacent field.

On Harvest Queen wheat grown under standard conditions about one-third of the leaves on the plants manifest comparatively few light-green to yellowish-green dashes, streaks, or bands parallel to the long axis of the leaf (fig. 12), sometimes running nearly the entire length of the leaf and the margins blending into the normal green tissue. Typical mosaic mottling is rare. It is often difficult to detect

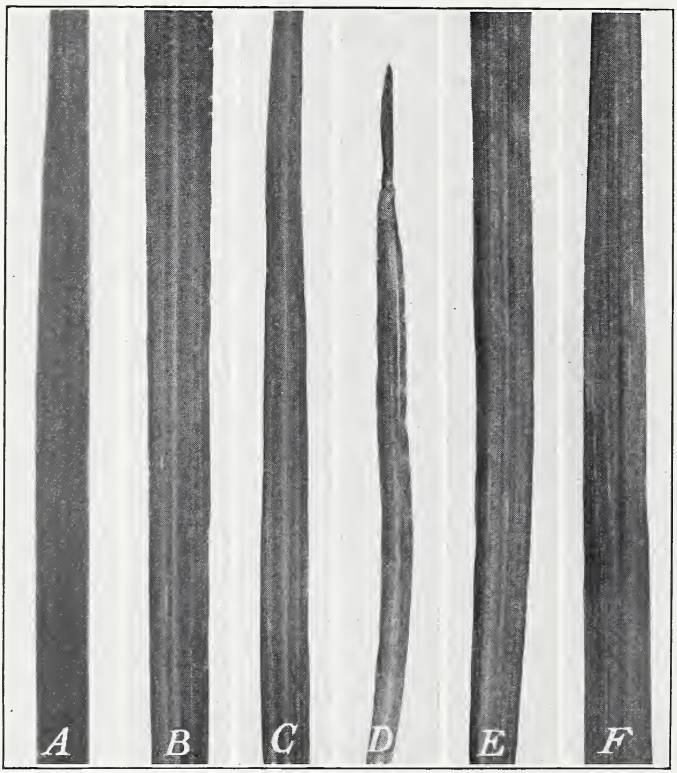

FIGURE 12.—Portions of leaves of Harvest Queen wheat, illustrating the foliage symptoms induced by mild streak mosaic (virus 6) under standard conditions on plants in the tiller-formation stage: *A*, Healthy leaf; *B*, *C*, *D*, and *E* illustrate the long streaks or bands of light-green tissue; *B*, *E*, and *F* illustrate shorter and narrow greenish-yellow streaks. Similar patterns appear on the leaves during the jointing stage.

definite mosaic mottling, stripes, or streaks when the plants are in the advanced jointing stage, but the leaves show irregular yellow-green patches which blend gradually into the slightly greener patches. This virus stunts the plant slightly, but does not cause rosette.

At 70° to 75° F., with a 14- to 15-hour day, the chlorotic zones are more yellow than under the above conditions. Under standard conditions virus 6 reduces the chlorophyll in the chlorotic areas much less than does virus 3 and to about the same degree as virus 4, but the total chlorotic area is much less in the case of virus 6.

YELLOW STREAK MOSAIC (WHEAT VIRUS 7) [10]

Wheat virus 7 was isolated from wheat collected at Salina, Kans. It was associated with virus 6 in the same tissue.

On Harvest Queen wheat grown under standard conditions 95 to 100 percent of all the leaves show greenish-yellow to extremely yellow dashes, streaks, stripes, or bands parallel to the long axis of the leaf, as illustrated in figure 13. Usually from 10 to 20 percent of the

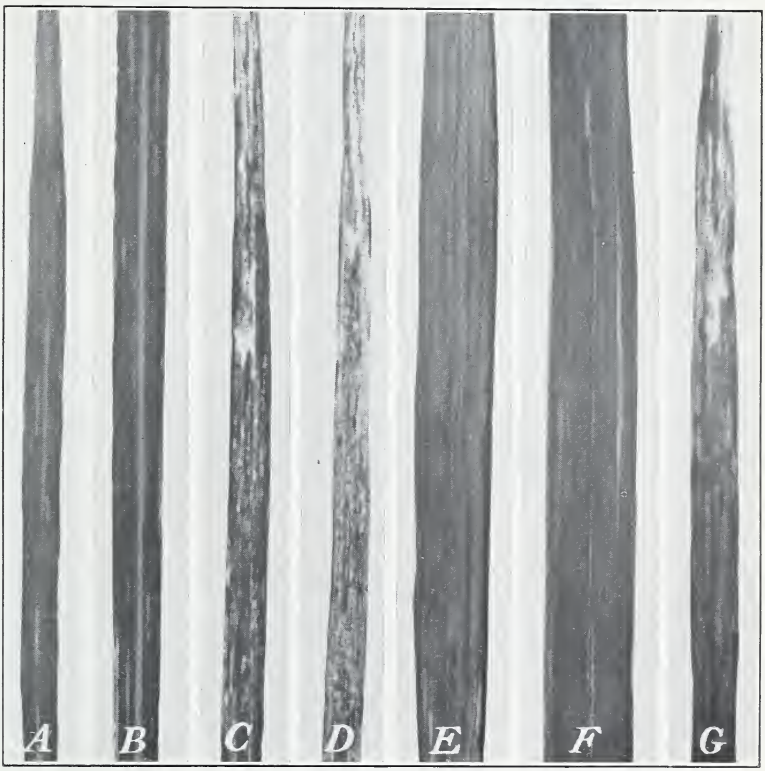

FIGURE 13.—Portions of leaves of Harvest Queen wheat, illustrating the foliage symptoms induced by yellow streak mosaic (virus 7) under standard conditions. Healthy leaf in figure 12 serves as the control for this figure. *A*, *B*, *C*, and *D* illustrate the symptoms during the tiller-formation period; *A* and *B* illustrate streaks which are more yellow than similar leaves illustrated in figure 12; *C* and *D* illustrate yellow mottling; *E*, *F*, and *G* illustrate mottling and streaking on leaves during the jointing period.

diseased leaves show distinct yellow chlorosis. Virus 7 does not reduce the amount of chlorophyll in the chlorotic areas so much as do viruses 3 and 5, but in general it causes a greater reduction of chlorophyll than viruses 4 and 6 when tested under standard conditions. In the early stages the symptoms induced by viruses 6 and 7 are difficult to distinguish, but within 2 to 4 weeks after the appearance of symptoms virus 7 will have induced a greater destruction of the chlorophyll in a larger portion of a given leaf and in a greater number of leaves than virus 6. Virus 7 induces more evidence of typical mosaic mottling (fig. 13, *C*, *D*, *E*, *G*) than does virus 6.

[10] In addition to the seven viruses listed, the virus of southern celery mosaic (celery virus 1) has been transmitted experimentally to wheat by Wellman (*19*). To what extent this virus may induce mosaic in wheat under natural conditions is not known.

During the jointing period under standard conditions yellow mottling, streaking, and striping become less apparent, but the plants show a general chlorotic condition and more mottling than are induced under these conditions by virus 6. Virus 7 stunts, but it rarely, if ever, kills the plant and does not induce rosette.

NATURE OF THE MOSAIC VIRUSES

Because the viruses of the grass mosaics are relatively difficult to study, most of the investigations on the nature of viruses have been carried out with the virus of the common mosaic of tobacco. Mosaic viruses have never been identified under the highest powered compound microscopes. Many of them pass through filters which prevent the passage of the smallest known bacteria. They regenerate in the living plant, but no one has succeeded in increasing them outside of the living plant.

The fact that viruses do regenerate in the living plant has been considered as evidence that they are organisms. On the other hand, certain chemical compounds and enzymes are generated by means of autocatalysis, a purely chemical mechanism. Some workers consider that the viruses are proteins (*15*) or closely associated with proteins (*16*, *1*).

In other papers (*7*, *8*) the writer has taken up the subject of virus mutation and the possible nature of the virus. In one of these (*8*) it is pointed out that even though the virus of tobacco mosaic may be a complex protein, it appears to possess a comparatively simple type of inheritance mechanism suggesting that the virus and its mutants may reflect a series of closely related compounds which function essentially as genes.

DISCUSSION

While all of the wheat viruses described are thought to be different, no attempt is made to decide whether the differences are of the magnitude of a species, variety, strain, race, isomere, polymere, or some greater or lesser categorical group. Therefore, the present grouping of the seven viruses can be considered only tentative, as it seems likely that further studies will suggest new arrangements. Although some of the characters now used serve to distinguish between plant viruses, ultimately they may be found to be only of minor importance and of no more value in a basic scheme of classification than is the fingerprint character in the present zoological classification of the primates. While it may be that no two viruses are identical in all particulars just as no two humans are exactly alike, and, as Mathews (*13*, *p. 216*), states "it probably is the case that even the proteins of two brothers are never identical", it is only reasonable to believe that there are certain fundamental characters which will be found to serve as a basis for grouping viruses into a rational taxonomic system. While some of these characters will doubtless be determined by physical and chemical methods applied directly to the viruses, it seems safe to predict that other characters will be based on biological reactions, such as symptom manifestations in suitable plant species and genotypes grown in suitable environments, and on other reactions, such as vector relationships or serological reactions.

As in the case of the tobacco mosaics, it is possible that many more viruses will be found to cause mosaics in wheat and that the wheat

viruses mutate. The green mosaic-rosette virus (virus 1) has been maintained through 43 subinoculations during 6 years. The light-green mosaic (virus 4) has been maintained through 33 subinoculations during 5 years. In the case of each mosaic the virus used for each subinoculation was obtained from plants developing the symptoms typical for the mosaic in question. The majority of the plants that become infected with these viruses manifest the typical symptoms at temperatures near 60° F. with 8 hours of light daily, but occasionally a plant or a leaf on a plant developed a distinctly yellow mosaic. Such expressions of yellow mosaic may represent mutations comparable to those known to occur in the common mosaic of tobacco.

In the early studies on the separation of wheat virus 1 from wheat virus 3 it was possible to obtain high percentages (80 to 100 percent) of infection in Harvest Queen wheat with wheat virus 1, but as the studies progressed it became increasingly difficult to obtain these high percentages, and in some inoculation tests no infection occurred. On the other hand, the other wheat viruses studied continue to induce fairly high percentages of infection, as shown in table 1.

It has not been possible to explain this infection decline on the basis of the plant material, the inoculation methods, or the environmental conditions. The most logical explanation at present is that unconsciously we have been selecting a virus that has a lower infection factor than was possessed by the original virus of mosaic-rosette. Such a virus may represent a mutant which arose before or during the period of study. If a virus is mutating it will be difficult to maintain certain characteristics over a long period of time when the virus transfers are made from selected leaves.

SUMMARY

Mosaics are known to occur on winter wheat in 44 counties in 7 States in the United States.

The distribution of these diseases is becoming more extended each year, and while they are very destructive under certain conditions there is no cause for alarm because some of these mosaics are controlled by means of resistant or tolerant wheats.

All tests conducted thus far have shown that the viruses occurring east of the Mississippi River are carried in some manner in the soil, the new wheat crop becoming infected therefrom.

Tests which have been made with soils from the mosaic-infested areas west of the Mississippi River have given no evidence that the viruses are carried in the soil.

Seven wheat mosaics considered distinct are described at temperatures near 60° F. with a daily photoperiod of 8 hours. These conditions are taken as standard because the winter-wheat plant responds in an essentially normal manner during the tiller-formation period and because the mosaic symptoms are comparable to those occurring in the field during the early spring growth period. The characteristics of these mosaics are summarized.

The viruses were purified in some cases from mixtures, by selecting tissues or plants showing symptoms differing from a given type and using these for virus in subsequent inoculations. Successive selection inoculations eventually yielded viruses that induce the new symptoms with a high degree of regularity.

TABLE 1.—*Synopsis of the salient features of the wheat-mosaic viruses described*

Name of mosaic, virus number, and point of collection	Time from inoculation to signs of mosaic	Infectivity	Symptoms 3 to 4 weeks after first signs of disease on Harvest Queen wheat grown near 60° F. with a daily photoperiod of 8 hours; "standard conditions"	Remarks
	Days	*Percent*		
Green mosaic or mosaic-rosette; wheat virus 1; Granite City, Ill.	21 to 45	0 to 45; average=16	Mild light-green mottling, short dashes or streaks, and sometimes long streaks or bands followed by an excessive amount of chlorophyll which obliterates the chlorotic areas. Rarely more than 10 percent of the leaves show signs of mottling at one time. Excessive development of tillers and stunting causes rosette about 3 weeks after the first sign of mottling.	Mottling occurs at 50° F. and at 70° to 75°, but no rosette symptoms appear. At temperatures near 60° typical rosette is inhibited or reduced when daylight intensity is poor and when the daily photoperiod is over 12 hours, but mosaic does develop. On Red Winter spelt a mild yellow mosaic occurs at 60° with an 8-hour day, but no rosette appears. No symptoms develop on *Agropyron repens*. Virus carried in some manner in the soil.
Green mosaic; wheat virus 2; Arlington, Va.	27 to 44	60 to 87; average=72	Very mild light-green mottling which is most evident in leaves which are emerging from the sheaths, especially in and near the unrolled portions of the leaves. Mottling seldom evident more than a short time after the complete emergence of the leaf. No excessive development of chlorophyll apparent and no rosette symptoms, thus distinguishing this virus from virus 1.	On *Agropyron repens* the symptoms are the same as on Harvest Queen wheat. Virus carried in the rhizomes.
Yellow mosaic; wheat virus 3; Granite City, Ill.	16 to 40	16 to 100; average=68	From 95 to 100 percent of all leaves show symptoms ranging from mosaic mottling, streaks, and stripes to almost complete yellowing. Usually from 25 to 40 percent of the diseased leaves show yellowing to some degree and the remainder exhibit light-green to yellow-green patterns. Many dead leaves at bases of plants. Young leaves sometimes are rolled, resembling leaves of wild garlic. Plants stunt in varying degrees and sometimes die prematurely, but rosette does not develop.	On Red Winter spelt a severe yellow mosaic develops at 60° F. in an 8-hour day. No symptoms develop on *Agropyron repens*. Virus is carried in some manner in the soil.
Light-green mosaic; wheat virus 4; Manhattan, Kans.	---do----	0 to 100; average=68	About 70 to 90 percent of the leaves on a plant show light-green to yellowish-green chlorosis frequently involving all or a large portion of the leaf. A few normal green dashes or streaks occur in the light-green areas, and light-green dashes and streaks develop in the darker green marginal zones which blend into the lighter areas. In a few leaves mottling develops in these marginal zones. Chlorophyll is reduced slightly more in the chlorotic areas than is the case with viruses 1 and 2. Long streaks, stripes, and bands, such as are associated with viruses 6 and 7, are unusual. Short yellowish streaks may appear on leaves of jointing plants. Virus stunts but does not kill the plants and does not induce rosette.	At 70° to 75° F. in a long day this virus induces a decided yellow mosaic on Harvest Queen wheat which is more pronounced than that induced by virus 6 under these growing conditions. No symptoms develop on *Agropyron repens*. No evidence that the virus is carried in the soil.

Yellow mosaic; wheat virus 5; Manhattan, Kans.	16 to 30	5 to 85; average=46	Symptoms are very similar to those induced by virus 3. They show in 95 to 100 percent of all the leaves, and 50 to 60 percent of these develop intensely yellow mottling, streaking, and striping to almost complete yellowing. Plants become badly stunted and frequently killed. The most severe of the yellow wheat mosaics. Does not induce rosette.	No symptoms develop on *Agropyron repens*. No evidence that the virus is carried in the soil.
Mild streak mosaic; wheat virus 6; Salina, Kans.	do	20 to 100; average=79	About one-third of the leaves on a plant show comparatively few light-green to yellowish-green dashes, streaks, or bands sometimes running the entire length of the leaf. The bands blend into the normal green tissue. Typical mosaic mottling is rare; plants are stunted but not killed; no rosette develops.	At 70° to 75°F. with a 14- to 15-hour day on Harvest Queen wheat the yellow areas are a little more conspicuous than at lower temperatures with shorter days. No symptoms develop on *Agropyron repens*. No evidence that the virus is carried in the soil.
Yellow streak mosaic; wheat virus 7; Salina, Kans.	13 to 30	40 to 100; average=84	From 95 to 100 percent of all leaves show greenish-yellow to extremely yellow mottling, dashes, streaks, stripes, or bands. Usually 10 to 20 percent of the diseased leaves show distinctly yellow chlorosis occurring in the several patterns mentioned. This virus does not reduce the chlorophyll in the chlorotic areas as much as do viruses 3 and 5, but it causes a greater reduction than viruses 4 and 6. Plants are stunted but rarely killed and do not develop rosette.	No symptoms develop on *Agropyron repens*. No evidence that the virus is carried in the soil.

The fact that some of the green wheat mosaics continue to express a small amount of yellow mosaic suggests that some of the viruses may be mutating, as in the case of the common mosaic of tobacco.

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